THE CRETACEOUS AMMONITE *AMMONITES REQUIENIANUS* D'ORBIGNY, 1841

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ABSTRACT. *Coilopoceras requienianum* (d'Orbigny, 1841) is revised on the basis of the types and other material. It shows wide intraspecific variation and dimorphism of the type demonstrated in North American species of the genus. Similar dimorphism is shown in other Old World species, especially Nigerian forms, with *Glebosoceras* Reyment, 1954, a strongly ornamented genus which is treated as a synonym of *Coilopoceras* Hyatt, 1903. The *Coilopoceras* from Algeria described by Pervinquière (1910) and said to be of Cenomanian age are confirmed as members of the genus, but they are shown to be upper Turonian; so this occurrence does not contradict previous views that the genus arose during the Turonian via *Hoplitoides* von Koenen, 1898.

AMERICAN species of the late Cretaceous ammonite genus *Coilopoceras* Hyatt, 1903, as well as the genus and family, have recently been reviewed by Cobban and Hook (1980), but *Ammonites requienianus* d'Orbigny, 1841, the first described species of the genus and its chief Old World representative, is poorly known. Restudy of d'Orbigny's types and other material in early collections allows us to give a reasonably full description of the ontogenetic development, variation, and dimorphism in the species. These accord with that shown by American species, and lead to an examination of other problematic Old World forms.

SYSTEMATIC PALAEONTOLOGY

Repositories of specimens. BM(NH), British Museum (Natural History), London; EMP, École des Mines, Paris, Collections now housed in the Université Claude-Bernard, Lyon; FSL, Faculté des Sciences, Université Claude-Bernard, Lyon; MNHP, Muséum National d'Histoire Naturelle, Paris; SP, Collections of the Sorbonne, now housed in the Université Pierre et Marie Curie, Paris.

Dimensions. Dimensions are given in millimetres, in the following order; diameter (D), whorl breadth (Wb), whorl height (Wh), and breadth of umbilicus (U); c = costal, ic = intercostal. Figures in parentheses refer to dimensions as a percentage of diameter.

Suture terminology. The suture terminology of Wedekind (1916; see Kullman and Wiedmann 1970) is followed here; I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894
Family COILOPOCERATIDAE Hyatt, 1903

[= Hoplitoidinae Wright, 1952, *nom. correct. ex* Hoplitoidinés H. Douvillé, 1912]

Genus COILOPOCERAS Hyatt, 1903, p. 91

Synonyms. Namadoceras Vredenberg, 1907; *Glebosoceras* Reyment, 1954.

Type species. Coilopoceras colleti Hyatt, 1903, p. 91, pl. 10, figs. 5–21; pl. 11, fig. 1.

Diagnosis. Large, up to 800 mm in diameter; involute, compressed to inflated, lanceolate to cordate in section, with more or less sharp venter; variable broad low ribs may or may not persist; in inflated forms (*Glebosoceras*) they are raised into large bulges on the inner part of the flank on outer whorls;

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in some such forms ribs may strengthen into ventrolateral nodes. Suture variable; accessory saddle may exceed in size the second lateral saddle, with auxiliary saddles tending to become entire in outline. Dimorphic: one member of pair compressed and feebly ornamented, the other more inflated and ribbed.

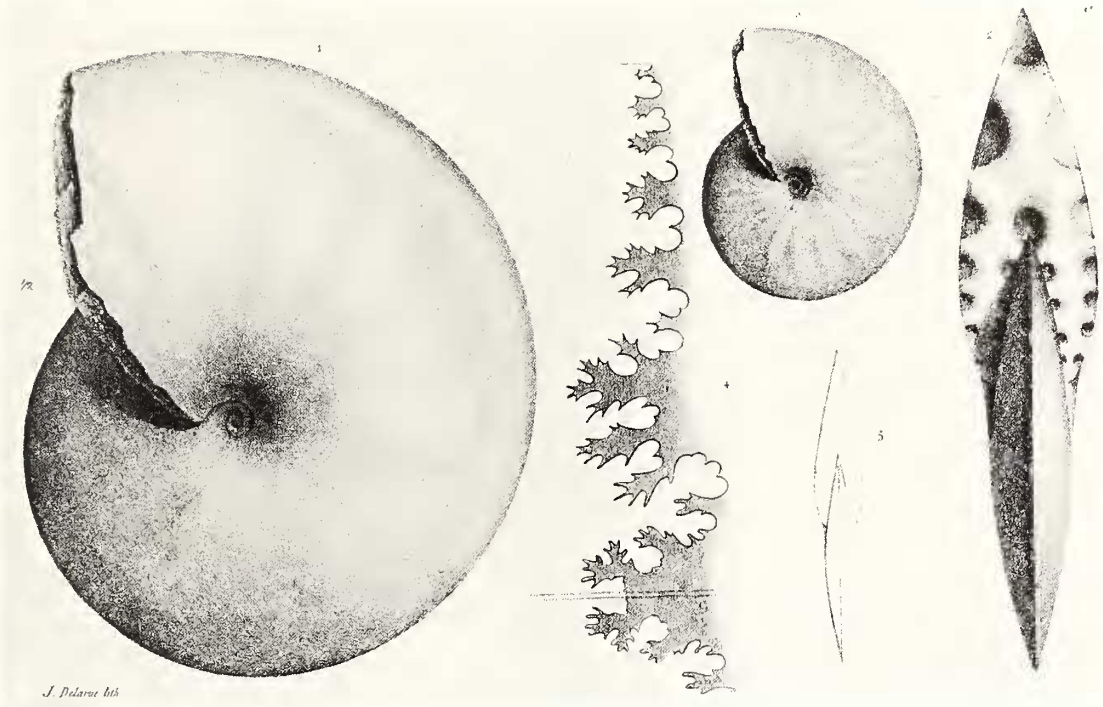
Discussion. Cobban and Hook (1980) provided a detailed account of the type species and other North American *Coilopoceras*. They demonstrated convincingly the succession from *Hoplitoides sandovalensis* Cobban and Hook, 1980, in the lower part of the upper Turonian *Prionocyclus hyatti* Zone, to *C. springeri* Hyatt, 1903 in the upper part of the same Zone. *C. springeri* and *H. sandovalensis* are indistinguishable when adult, and only the acute venter of the early stages of the former and the tabulate venter of the early stages of the latter serve to distinguish them. *C. springeri* gave rise to *C. colleti* Hyatt, 1903, of the succeeding *P. macombi* Zone. This species develops distinctive ventrolateral tubercles when adult (see Cobban and Hook 1980, text-fig. 9). Juveniles have only incipient tubercles, with the ends of the ribs projecting and accentuated. They also differ in sutural characteristics: in *C. colleti* L/U_2 is asymmetrically bifid; in *C. springeri* the three divisions of the ventral half of this lobe enlarge so that there are five large lobules rather than two. The youngest American species is *C. inflatum* Cobban and Hook, 1980. This is very inflated indeed and also develops tubercles (see Cobban and Hook 1980, text-fig. 14). In all these species Cobban and Hook demonstrated the presence of both slender, feebly ornamented and stout, strongly ribbed forms which they regard as dimorphs, a view followed here. They were unable to show a size difference between adults of the two forms, so that the two morphs cannot yet be identified as microconch and macroconch. As is shown below under the systematic description of *C. requienianum*, the same variation and dimorphism can be demonstrated in this Old World member of the genus.

Occurrence. Upper Turonian of France, Germany, North and West Africa, Madagascar, Israel, Lebanon, Baluchistan, Colorado, Wyoming, Texas, New Mexico, Mexico, Trinidad, Ecuador, Colombia, and Peru.

Coilopoceras requienianum (d'Orbigny, 1841)

Plates 35, 36; text-figs. 1–5

1841 *Ammonites Requienianus* d'Orbigny, p. 315, pl. 93, figs. 1–4.
1894 *Sphenodiscus Requieni* d'Orbigny sp.; de Grossouvre, p. 140, text-fig. 59.
?1896–1897 *Sphenodiscus Requieni* (d'Orbigny); Peron, p. 34, pl. 17(4), figs. 2, 3; pl. 11(17), fig. 4.
1903 *Coilopoceras requienianum* (d'Orbigny); Hyatt, p. 99.
1903 *Coilopoceras? grossouvrei* n. sp. Hyatt, p. 100, pl. 12, fig. 7.
1904 *Sphenodiscus Requieni* d'Orb; Solger, text-fig. 74 (*pars*) (after de Grossouvre).
1907 *Sphenodiscus Requieni* d'Orbigny; Pervinquière, p. 221, text-fig. 90.
1907 *Sphenodiscus Requienianus* (d'Orbigny); Boule, Lemoine and Thévenin, text-fig. 27B (copy of de Grossouvre).
?1912 *Coilopoceras Requieni* d'Orbigny; Douvillé, p. 308, text-figs. 36–38, 68.
1913 *Coilopoceras Requienianum* d'Orbigny; Roman and Mazeran, p. 28, pl. 3, fig. 5; text-figs. 5, 6.
1938 *Coelopoceras* (sic) *Requieni* (d'Orbigny); Roman, p. 499, pl. 51, figs. 477, 477*a* (copy of d'Orbigny).
?1941 *Coelopoceras* (sic) *requieni* (d'Orbigny); Chiplonkar, p. 274, text-fig. 6 (indeterminate).
1952 *Coilopoceras requienianum* (d'Orbigny); Basse, p. 665, fig. 30 (copy of d'Orbigny).
1958 *Coilopoceras requienianum* (d'Orbigny); Luppov and Drushchits, p. 130, text-fig. 103*d* (copy of Roman 1938).
?1965 *Coilopoceras requieni* d'Orb.; Collignon, p. 24, pl. 385, fig. 1658 (indeterminate from figure).
?1975 *Coilopoceras* cf. *requieni* (d'Orbigny); Dassarma and Sinha, p. 70, pl. 9, fig. 6; pl. 12, fig. 5 (indeterminate).
1976 *Coilopoceras requienianum* (d'Orbigny); Lommerzheim, p. 231, pl. 2, fig. 4; text-fig. 10*a–c*.
non 1977 *Coilopoceras requieni* (d'Orbigny); Gonzalez-Arreola, p. 170, fig. 2*d*, *e*.
?1981 *Coilopoceras requieni* d'Orbigny; Obata, Kanie, Ranaivoson and Ratsimba, pl. 1 (indeterminate from figures).



TEXT-FIG. 1. *Ammonites requienianus* d'Orbigny, 1841 (pl. 93). Copy of d'Orbigny's original figures.

Types. D'Orbigny must have had a series of specimens before him when erecting this species, for in his explanation of the plate (1841, p. 317), which is reproduced here in text-fig. 1, he states as follows: 'Pl. 93, fig. 1, Individu réduite de moitié, vu de côte. De la collection de M. Requien et de la mienne. Fig. 2. Le même, vue de côté de la bouche, montrant le dessus d'une cloisone. Fig. 3. Un jeune de la variété ondulée. Fig. 4. Une cloisone de grandeur naturelle, calquée par moi sur la nature.' The larger specimen in the Requien Collection was re-illustrated by Roman and Mazeran (1913, text-fig. 5) and referred to as the 'type'; this is not, however, a valid lectotype designation. The posthumous catalogue of the d'Orbigny Collection lists thirteen specimens from Uchaux, Vaucluse, and fourteen are in the collections under the number 6775. All of these specimens rank as syntypes; the Requien specimen refigured by Roman and Mazeran is here designated lectotype; the paralectotypes are all rather poorly preserved and none demonstrably agree with d'Orbigny's pl. 93, fig. 3. A selection of the better specimens are refigured in text-fig. 2.

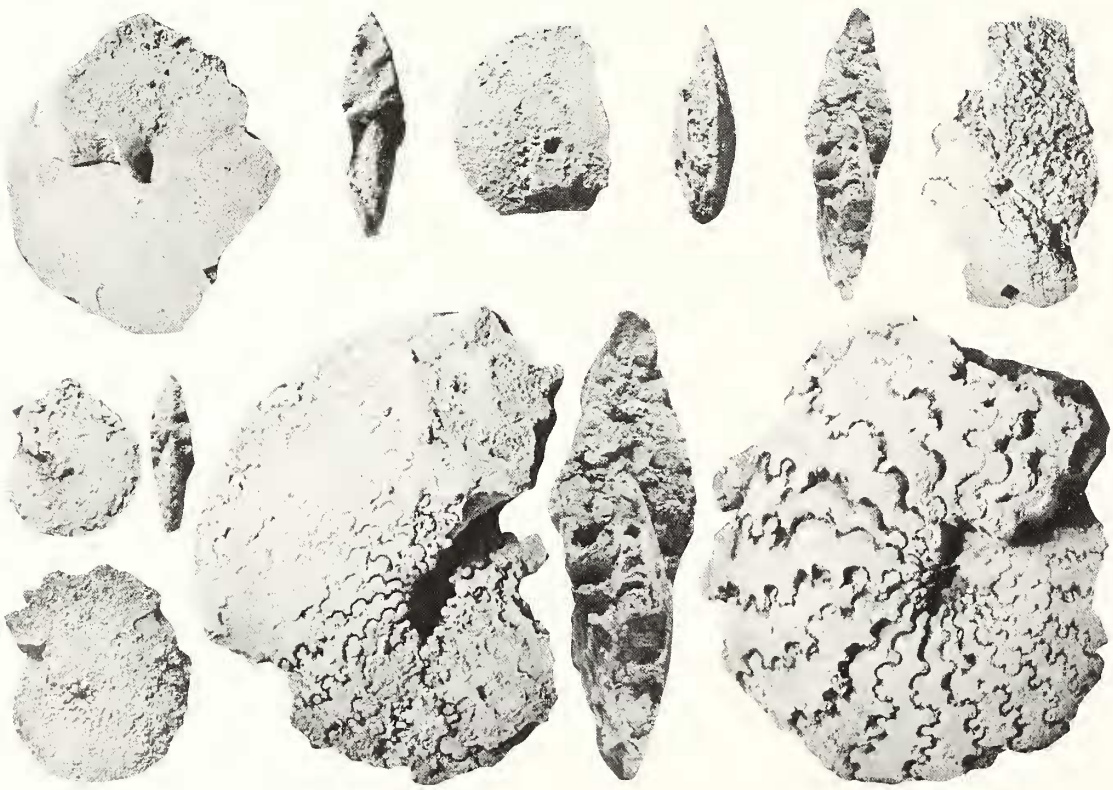
Material. We have studied nearly fifty specimens in the EMP, FSL, MNHP, SP, Université de Marseilles, and other French collections, all from localities in the Uchaux Massif, and variously labelled 'Colline de Boncavail', 'Uchaux', or 'Mondragon'. One specimen in the SP collections is from the Tuffeau Jaune de Touraine of Courtinot, Touraine (Hébert Collection); Oxford University Museum no. KZ15177 and specimens in J. M. Hancock's Collection are from the Tuffeau Jaune at Vreigne, near Francueil, Indre-et-Loire.

Description. The material occurs either as silicified nuclei, some of which retain the silicified dorsal shell layer and traces of the internal suture, or as sandstone moulds. The largest specimen we have seen is 200 mm in diameter.

Two forms of the species occur. At one extreme are smooth oxycones with a lanceolate whorl section and sharp venter (text-figs. 3, 4A). At the other are ribbed individuals which are generally stouter and a little more evolute (text-fig. 4B). Juveniles of the latter show pairs of low broad rounded primary ribs that are best developed on the inner flank but may also be accentuated on the ventrolateral shoulder before declining, while shorter intercalated ribs are also present. The largest ribbed variant is shown in Plate 36, fig. 12. There are six strong

umbilical bulges per whorl, which give rise to pairs of coarse broad primary ribs, and single shorter intercalated ribs. These strengthen before terminating abruptly, and there is a smooth zone on either side of the venter, which is acutely fastigiate. The siphuncle is very large. The suture line is shown by relatively few specimens (text-fig. 5). E is broad and shallow; L very broad, open, and symmetrically bifid. The saddle E/L is squat, with broad rounded frills, as is L/U_2 and the minor saddles on the umbilical lobe.

Dimensions	D	Wb	Wh	Wb : Wh	U
FSL 14.200d	23·9(100)	6·4(26.8)	13·3(55.6)	0·48	— (—)
FSL 14.200c	26·5(100)	8·0(30·1)	15·2(51·4)	0·53	1·0(3·7)
FSL 14.200a	64·0(100)	14·6(22·8)	36·3(56·7)	0·42	2·3(3·6)
FSL 14.201	51·0(100)	16·0(31·4)	27·6(54·1)	0·58	2·8(5·5)
FSL 14.200e	79·0(100)	19·8(25·0)	44·6(56·5)	0·45	2·1(2·7)
FSL 14.202	94·4(100)	22·1(23·4)	50·5(53·5)	0·44	— (—)
SP Pervinquière Coll.	93·7(100)	24·0(25·6)	52·4(55·9)	0·46	2·8(3·0)
SP Toucas Coll.	136·0(100)	31·8(23·4)	72·1(53·0)	0·44	— (—)
SP 'Mondragon' c	165·0(100)	38·0(23·0)	74·5(45·1)	0·51	18·0(10·9)
ic	165·0(100)	42·0(25·5)	74·5(45·1)	0.56	18·0(10·9)
FSL 14.210	170·0(100)	40·0(23·5)	94·5(55·6)	0.42	8·5(5·0)



TEXT-FIG. 2. *Ammonites requienianus* d'Orbigny, 1841. MNHP 6775 (d'Orbigny Collection), seven of the better preserved paralectotypes, all of which are silicified and from Uchaux (Vaucluse). All × 1.

Discussion. C. requienianum is best known from the Uchaux region, but has been recorded from Touraine by several authors. The specimens we have seen include both ribbed and smooth individuals and have similar sutures. Hyatt (1903, p. 100) renamed the specimen from Usseau (Vienne), of which de Grossouvre (1894, text-fig. 59) illustrated the suture line, *C.? grossouvrei* because of differences in detail from the suture figured by d'Orbigny. Comparison of d'Orbigny's figure with the lectotype and other Uchaux specimens shows d'Orbigny's figure to be highly misleading with its very long narrow elements.

The presence of ribbed and smooth forms within *Coilopoceras* species has already been described in both the type species, *C. colleti* Hyatt, 1903, and the slightly later *C. springeri* Hyatt, 1903 and *C. inflatum* Cobban and Hook, 1980 (see Cobban and Hook 1980 for a full review of these species), and treated as dimorphism; the proportions of the two morphs are variable. As yet it is not known whether this difference in ornament is accompanied by a size difference. *C. requienianum* can be distinguished from these American species chiefly on the basis of the suture line (text-fig. 5); in *C. colleti* E/L is narrower and much more deeply incised, with elongate rather than squat frills, as well as asymmetrically bifid, while the inner lobes and saddles are also more incised. In *C. springeri* the saddles are even more incised with narrow stems, while E/L is very broad and asymmetrically trifid. *C. inflatum* Cobban and Hook, 1980 (p. 19, pl. 1, figs. 9–11; pl. 11, fig. 2; pls. 12–17; pl. 18, figs. 1–3, 11–13; pls. 20, 21; text-figs. 14, 15) has similarly distinctive sutures, is far more inflated than any known *C. requienianum*, and develops ventrolateral tubercles.

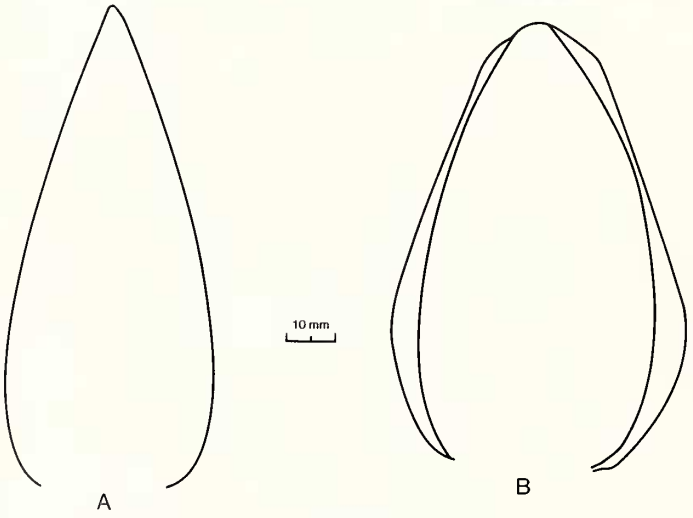
The above species and *C. requienianum* are the only ones in which a reasonable number of specimens has been described. As Cobban and Hook (1980) noted, at least twenty-seven species in addition to the American forms have been described. We agree with them that the groups of species described from single horizons and localities and separated on details of suture and ornament probably represent no more than single variable species. Particularly relevant to this issue is *C. requienianum altesellata* Collignon, 1965 (p. 62, pl. 403, figs. 1688, 1689; p. 64, pls. 404, 405) from the upper Turonian of Madagascar. Collignon referred a series of smooth forms to this 'variety', which he differentiated from the nominate form on the basis of the saddle E/L; this is narrow, deeply incised, and like that of the American forms noted above. It appears to be a distinct species and, interestingly, occurs with stouter ribbed specimens identified as *Glebosoceras glebosum* Reyment, 1954 (Collignon 1965, p. 60, pl. 402, figs. 1686, 1687). These have the same sutural peculiarity, and we again take them to be a dimorphic pair. *G. glebosum* Reyment, 1954 (p. 161, pl. 2, fig. 3; pl. 4, fig. 1; text-fig. 5; Reyment 1955, p. 75, text-fig. 35) from Nigeria has a similar suture line to *C. discoideum* Barber, 1957 (p. 55, pl. 2, fig. 1; pl. 3, figs. 1, 2; pl. 25, figs. 1–4) according to Barber, and they may be a further pair. Certainly, *Glebosoceras* is no more than an inflated *Coilopoceras*.

Occurrence. The type material is from the Uchaux Massif, where it is an upper Turonian *Subprionocyclus neptuni* Zone species. It is also known from scattered localities in the upper Turonian Tuffeau Jaune of Touraine, occurring at Usseau (Vienne) (de Grossouvre 1894), Courtinot (Touraine), and Vreigne, near Francueil (Indre-et-Loire). Lommerzheim (1976) has recorded a fragment from the condensed Turonian of Mulheim (Westphalia) that may belong here. The North African material whose sutures were illustrated by Douvillé (1912) are only doubtfully referable to the species.

DISCUSSION

Observations on *C. requienianum* show that compressed feebly ornamented and more inflated ribbed forms occur side by side, as in the North American type species and wherever *Coilopoceras* occurs. Cobban and Hook (1980, p. 5) accepted *Glebosoceras* as a distinct genus on the grounds that the ribs bend sharply forward on the outer part of the flank. A re-examination of the holotype, BM(NH) C47336, shows that this is a pathological condition. The forward projection is shown only by the third and fourth ribs of the figured side of the specimen (Reyment 1954, pl. 4, fig. 1) and is not a criterion for separation from *Coilopoceras*.

TEXT-FIG. 3. *Coilopoceras requienianum* (d'Orbigny, 1841). FSL 14.210, large specimen of compressed form from Uchaux, Vaucluse; 175 mm in diameter.



TEXT-FIG. 4. *Coilopoceras requienianum* (d'Orbigny, 1841). Whorl sections. A, compressed form, based on FSL 14.210 from Uchaux, Vaucluse. B, inflated form, based on an unregistered Sorbonne specimen from Mondragon, Vaucluse.

EXPLANATION OF PLATE 35

Figs. 1–6. *Coilopoceras requienianum* (d'Orbigny, 1841). 1–3, FSL 14.202, ribbed juvenile from the environs of Bollène (Vaucluse) (Sayn Collection). 4–6, a more compressed, feebly ribbed juvenile, Sorbonne Collections, labelled 'Mondragon ?' (Pervinquière Collection). All × 1.

1

2

3

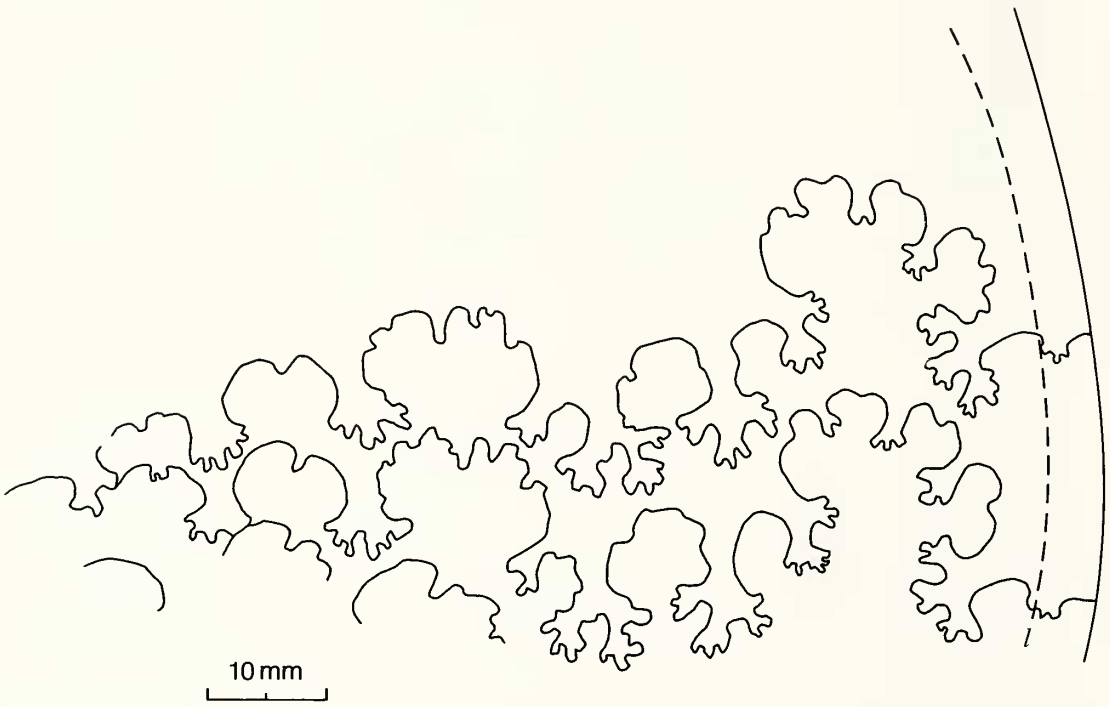
4

5

6

KENNEDY and WRIGHT, *Coilopoceras*

Cobban and Hook (1980) made it quite clear that *Hoplitoides* occurs in New Mexico in association with *Collignoniceras woollgari* (Mantell, 1822), that the earliest *Coilopoceras* in that area occurs with *Prionocyclus hyatti* (Stanton, 1894), and that later forms of *Coilopoceras* occur with *P. macombi* Meek, 1876 and *P. wyomingensis* Meek, 1876. This dating does not agree with the general recording of *Hoplitoides* as lower Turonian, and in particular Reyment's (1954, 1955) and Barber's (1957) records from Nigeria of *Hoplitoides* as 'lower Turonian' and *Coilopoceras* as 'lower Turonian (*Paravascoceras* horizon)' or even earlier (Barber 1957, p. 59). Careful reading of these papers, however, shows remarkably few cases of actual associations of specimens of either genus with other genera; neither appears in the only measured section, at Pindiga (Barber 1957, p. 60). The only definite reference appears to be to the occurrence in 'the limestone near Makurdi' of various *Hoplitoides* and *C.*(?) sp. with *Mammites mutabilis* Reyment, 1955, *Benueites*, and *Kamerunoceras jacobsoni* Reyment, 1955. None of these are yet known to entail any definite horizon within the Turonian. Otherwise, all the records of *Hoplitoides*, *Glebosoceras*, and *Coilopoceras* in Nigeria are from imprecise horizons which may cover several zones.



TEXT-FIG. 5. *Coilopoceras requienianum* (d'Orbigny, 1841). External sutures from an unregistered specimen, Sorbonne Collections (*ex* Pervinquière Collection).

EXPLANATION OF PLATE 36

Figs. 1–12. *Coilopoceras requienianum* (d'Orbigny, 1841). 1–3, FSL 14.200b, almost smooth juvenile. 4–6, FSL 14.201, a more inflated, ribbed juvenile, the original of Roman and Mazeran (1913, pl. 3, fig. 5). 7, 8, FSL 14.200c. 9–11, FSL 14.200d, smooth nuclei. 12, the most strongly ornamented specimen seen, Sorbonne Collections. 1–11 are labelled 'Uchaux', 12 'Mondragon', both in Vaucluse. All ×1.

KENNEDY and WRIGHT, *Coilopoceras*

In Peru (Benavides-Cáceres 1956), *Coilopoceras* is recorded as common. One new species, *C. jenksi*, is said to be the commonest species in the Coñor Formation (ibid., p. 473), though is not listed among the fossils of that formation on p. 384. However, the Coñor Formation may be up to 200 m thick and, despite a statement (ibid., p. 473) that *C. jenksi* 'is usually associated with *Hoplitoides inca*, *Mammites nodosoides afer*, *Pseudaspidoceras reesidei*, *Thomasites fischeri*, *Broggiiceras olssoni*, and *B. humboldti*', we cannot see here any hard evidence for its relative dating; the 'associated' species cover *Paravascoceras* and *M. nodosoides* zones and, since they comprise all the ammonites listed from the whole Conõr Formation (ibid., p. 384), the biostratigraphic information is weak. Etayo-Serna (1979) included in his zonation of central Colombia a '*Mammites nodosoides appelatus–Franciscoites suarezi* Assemblage Zone' in which *Hoplitoides* occurs, but this Zone could in fact cover the whole Turonian. Abundant *Coilopoceras*, including *Glebosoceras*-like forms, in collections before us from Colombia (University of California Collection), are never associated with species of other genera.

A similar situation is found on close investigation of the many references to the occurrence of *Hoplitoides* or *Coilopoceras* in the lower Turonian or earlier. In the case of the *Coilopoceras* described from the Cenomanian of North Africa by Pervinquière (1910), Reyment (1955, p. 75) suggested that they were schloenbachiids. However, Cobban and Hook (1980, p. 12) pointed out that the sutures of the Algerian species resemble those of true *Coilopoceras* in the general appearance of the first lateral lobe, but that the rest of the suture has only two or three lateral lobes. Part of the type material of both *C. africanum* Pervinquière, 1910, and *C. haugi* Pervinquière, 1910 is refigured here (Pl. 37, figs. 1–12); they are not schloenbachiids. *C. africanum* has a broadly bifid first lateral lobe (but with a third subsidiary lobule) and *C. haugi* a trifid one, but in our view they belong to a single variable species. The more strongly ornamented specimens compare well with small specimens of *C. inflatum* (e.g. Cobban and Hook 1980, pl. 18, figs. 1, 2, 8) and we believe them to be true *Coilopoceras*, showing the same range in ornament and whorl section as other species. We doubt, however, the dating of this material. *C. africanum* is based on eight specimens and fragments said to be from the middle Cenomanian of Djebel Guessa and Berrouaghia, collected by Thomas and Peron; *C. haugi* on three complete specimens and a dozen fragments also said to be from the middle Cenomanian of Berrouaghia, also collected by Thomas and Peron. The '*Acanthoceras* cf. *Ac. Newboldi* Kossmat' of Pervinquière (1910, p. 45, pl. 13, fig. 37) was also collected by Thomas and is in the Peron Collection; it was said to be from the '2^e zone, moyenne' of Berrouaghia, but is a juvenile *Romaniceras* (*Romaniceras*) *deverianum* (d'Orbigny, 1841) (Kennedy *et al.* 1980, p. 330, pl. 39, figs. 7–10), a high Turonian species commonly associated with *Coilopoceras*. This suggests that the *Coilopoceras* too are misdated, while we have independent unpublished evidence that limonitic Turonian ammonites occur in the Berrouaghia–Aumale area of Algeria.

We are thus led to conclude that there is no strong evidence for the occurrence of *Hoplitoides* or *Coilopoceras* before the middle Turonian, although it is possible that the former's occurrences in West Africa are in rocks that are datable, at least in part, to the upper part of the lower Turonian. On this basis there is no longer any difficulty in accepting the evolution of *Coilopoceras* from *Hoplitoides* (Wright 1957, p. L425; Cobban and Hook 1980, p. 13).

EXPLANATION OF PLATE 37

Figs. 1, 2, 8–12. *Coilopoceras africanum* Pervinquière, 1910. 'Cotypes' from Djebel Guessa, Algeria, Sorbonne Collections.

Figs. 3–7. *Coilopoceras haugi* Pervinquière, 1910. 'Cotypes' from Berrouaghia, Algeria, Sorbonne Collections. All ×2.

KENNEDY and WRIGHT, *Coilopoceras*

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